The Skeletons of Recent and Fossil Gymnogyps

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A STUDY OF THE SKULLS of the cathartid vultures (Fisher, 1944: 272–296) revealed certain fundamental differences in the conformation and proportions of skulls of Recent *Gymnogyps californianus* and fossil *Gymnogyps* from the tar pits of the Rancho La Brea Pleistocene. Even though some of these differences were slight morphologically, their presence in areas of minimal variation such as the occipital ring of bones, the basitemporal area, and the posterior palatal region indicated that the Recent and fossil condors were not identical. Further, the magnitude of other differences and the absence of overlap in the ranges of certain significant measurements demonstrated that two species probably were involved.

Before that study was made, it was believed that the fossils from the Pleistocene of Rancho La Brea belonged to *californianus,* as did all Recent birds of this genus. There remained, however, the species *amplus,* from the Pleistocene deposits of Samwel Cave in northern California. Further study of *amplus* showed it to be conspecific with the Rancho La Brea specimens because the characters by which it had first been differentiated were shown to be identical in specimens from the two deposits. As a result, the name *californianus* was restricted to the living form of *Gymnogyps,* and *amplus* applied to all the Pleistocene specimens known from western North America.

It has been suggested that the two stocks of condors represent subspecies of the same species, i.e., chronological subspecies. There may be a chronocline with the mean size of the individuals of the population decreasing from Pleistocene to Recent times. If this be true for this species, as has been found for other warm-blooded species, the fact might illustrate Bergmann's rule in a temporal rather than a geographic way. Although this present analysis of the skeleton tends to bear out the belief that two subspecies are involved, it is still necessary to consider the major specific differences in the skulls, and to remember that the skeletal elements studied in this investigation are in general more plastic and more subject to the influence of external environmental conditions than are the bones of the skull. Thus, one would expect to find in these elements a greater similarity between the two series of specimens.

At present the only criteria by which these two species can be segregated are skull characters. Except in the oil deposits of southern California, fossil deposits seldom contain complete skulls of birds. Hence, it seemed desirable to obtain some means of separating the two species on the basis of other bony elements. For that reason, primarily, this study was undertaken. Secondarily, it seemed pertinent to test the often-repeated assumption that "Pleistocene forms are more variable than Recent forms." It has been noted previously that paleontological series of a species often do show considerable variability. This variability may be explained in two ways: (1) the fossil species actually is more variable; (2) the series is inadequate and heterogeneous because of age and sex factors that cannot be determined and because the series often comes from various localities and from deposits of different ages.

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The abundant series of *G. amplus* from the Rancho La Brea provided ample specimens for an adequate series from one locality of known age; no sub-Recent specimens were included. The Pleistocene tar pits may have operated over a period of several thousands of years, but of all the known avian-bearing horizons these are perhaps the most accurately restricted chronologically. The age factor was minimized by selecting well-ossified and completely fused bones for both the Recent and fossil series. Sexual variation is of minor importance in these condors because it was found (Fisher, 1946: 547) that the sexes of the Recent species do not vary significantly in their skeletal measurements; hence, in the present study the sexes were lumped. With these factors causing variability eliminated, any variation in the *amplus* series could result only from a certain inherent variability in the homogeneous stock, or possibly from inclusion of heterogeneous stocks trapped in the oil at various times during the Pleistocene. To measure this variability the coefficient of variation was calculated for each skeletal element studied.

Measurements and ratios of the several bones are presented in the tables. In these can be found some 3,000 measurements that were made with dial calipers. The range, the mean and its error, the standard deviation (σ) and its error, and the coefficient of variation (V) are given in Tables 1 to 14. Slight discrepancies are present in the third place of some of the figures because many of the computations were of necessity made with only a slide rule. The magnitude of the standard deviations was used to check the adequacy of the sample when compared to the observed range and mean. This check is based upon the fact that an observed range equal to 6σ approximates the real range and that an observed range of 4σ probably includes about 95 per cent of the real range, whereas an observed range of 2σ is about equal to 68 per cent of the actual range. The means were compared in various ways. For example, the formula d/σ was used in comparing the means of large samples, and the familiar "t" test was used in comparing smaller samples. In a few instances both tests were applied to a single element. The value σ_d may be obtained in two ways (Simpson and Roe, 1939: 192–193). Formula 1:

$$\sigma_d = \sqrt{\frac{N_1}{N_2}\sigma^2_{m_1} + \frac{N_2}{N_1}\sigma^2_{m_2}}$$

is designed to test the hypothesis that both the means and the variances are likely to be the same in the populations from which the two samples are taken. Formula 2:

$$\sigma_d = \sqrt{\sigma^2_{m_1} + \sigma^2_{m_2}}$$

is used to determine the possibility that the two series differ significantly in the mean of a variate, and it assumes that the sample estimates of variance are near the true population values. Needless to say, a significant test from either formula indicates that the populations are likely to be different. Because some workers prefer the first formula and others the second and because it is of considerable interest to note the varying results when the two formulae are applied to the same data, both formulae were used in this study, and the results of all the significance tests are given in Tables 15 and 16.

In addition to this statistical analysis, a careful qualitative comparison was made of each element available for the two species. This later comparison, however, proved valueless, for no skeletal elements other than those of the skull could be identified on the basis of qualitative characters alone. Thus the present paper is essentially a study of absolute and relative measurements, their variance, and their importance in identifying the species under study. However, the data presented may also be of use in future studies of the tempo and mode of evolution as defined and studied by Simpson (1944).

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TABLE 1

MEASUREMENTS OF THE WING (mm.)*

	NO. SPECIMENS	MEAN	MAX.	MIN.
Humerus	11	267	274	262
	60	276	292	260
Ulna	8	313	320	305
	31	322	345	304
Metacarpus	3	132	133	131
	118	139	148	129
Digit II, phalanx 1	6	53.4	54.0	52.1
	74	54.8	60.5	51.3
Digit II, phalanx 2	4	43.9	44.8	43.4
	26	50.2	52.7	47.0
Total length		809	826	794
		842	899	791

* First row of figures under each category pertains to *californianus,* the second row to *amplus.*

DISCUSSION OF MEASUREMENTS

In Table 1 the measurements of the wing demonstrate that the mean wing length of *amplus* is 4 per cent greater than in *californianus;* the maximum length in *amplus* is 8 per cent greater, but the minimum lengths are about the same. It should be noted, however, that the entire range of wing lengths in *californianus* is within the limits of the range of *amplus.* Consequently, the species could not be separated on the basis of wing length, even if associated skeletons of the fossil were available. A statistical study of the intramembral proportions of the wing shows no significant differences between the two species.

In no raw measurement (Table 2) of individual humeri do the species differ; in the series the fossil form is always largest, but all the ranges overlap considerably. Signifi-

TABLE 2

MEASUREMENTS (mm.) AND PROPORTIONS OF THE HUMERUS*

	NO. SPECIMENS	RANGE	MEAN	STANDARD DEVIATION	COEFFICIENT VARIATION
Total length	11	262–274	267±1.2	3.93± .84	1.47± .31
	60	260–292	276± .95	7.32± .67	2.65± .24
Greatest proximal width	13	48.2–53.3	50.3± .42	1.51± .30	3.00± .59
	52	50.2–57.5	53.7± .25	1.82± .18	3.39± .33
Greatest distal width	11	45.0–49.0	47.0	....	....
	59	46.4–54.6	49.8	....	....
Length bicipital crest	13	47.1–52.2	49.2	....	....
	50	48.0–55.9	51.6	....	....
Length deltoid crest	12	97–119	105±1.87	6.47±1.32	6.16±1.32
	59	113–129	120± .57	4.41± .41	3.67± .34
PROPORTIONS OF HUMERUS					
Proximal width : length	11	18.2–19.6	18.6± .13	.44± .09	2.33± .50
	52	18.1–20.6	19.5± .03	.20± .02	1.03± .10
Distal width : length	11	16.7–18.6	17.6	....	....
	59	17.3–19.1	17.8	....	....
Bicipital length : length	11	17.9–19.0	18.3	....	....
	50	17.6–20.1	18.8	....	....
Deltoid length : length	11	36.5–42.7	39.2± .64	2.12± .45	5.4 ±1.2
	59	40.4–46.8	43.6± .16	1.2 ± .11	2.75± .25

* First row of figures under each category pertains to *californianus,* the second row to *amplus.*

cance tests on humeral length, proximal width, and length of deltoid crest (Table 15) demonstrate that the means of the two series are significantly different. The ranges of all intramembral ratios calculated for the humerus overlap, but the significance tests show that the means are statistically different. The bone is in all dimensions heavier in the fossil. With the exception of the coefficient of variation for length of the deltoid crest, all these coefficients are greater in *amplus* than in *californianus*. The relatively greater V for this crest in the Recent species may be an indication that the length of the crest is now undergoing a change. Throughout Table 2 the standard deviations for measurements made on *californianus* indicate that the sample probably was sufficiently large to include 80 to 95 per cent of the actual range. On this same basis the sample of *amplus* was distributed over the range that would be expected for 90 per cent of the whole population.

Table 3 shows that absolute measurements of the ulna for the two series overlap in every instance. Significance tests on ulnar length indicate that there is 1 chance in 20 that the two series could have come from the same population; further, the means are significantly different. Tests (Table 15) on distal and proximal widths of the ulna revealed that means of the two series are statistically distinct. Raw ratios of a single ulna cannot be used to identify the species, but again the means of ratios for the two series are significantly different. As regards the ulna, the coefficient of variation in *amplus* is larger than in *californianus* in one instance, smaller in three, and about equal in another. Although the sample for the Recent condor was small, it probably includes about 80 per cent of the expected range of variation of the entire population.

The available number of metacarpal elements of the modern condor was too small for reliable treatment, but the metacarpus seems to be significantly longer in the fossil (Tables 5 and 15).

TABLE 4

LENGTH OF THE METACARPUS (mm.)*

Number of specimens	3 118
Range	131–133 129–148
Mean	132±.61 139±.37
Standard deviation	1.05±.43 4.06±.26
Coefficient of variation	.80 2.92±.19

* First row of figures under each category pertains to *californianus*, the second row to *amplus*.

TABLE 3

MEASUREMENTS (mm.) AND PROPORTIONS OF THE ULNA*

	NO. SPECIMENS	RANGE	MEAN	STANDARD DEVIATION	COEFFICIENT VARIATION
Length	8 31	305–320 304–345	313±1.75 322±2.2	4.96±1.24 12.2 ±1.55	1.58± .40 3.79± .48
Proximal width	8 25	28.9–32.7 32.2–36.7	31.1± .46 34.3± .28	1.30± .33 1.41± .20	4.17±1.05 4.11± .58
Distal width	8 28	16.1–25.0 23.6–27.9	20.6±1.39 25.8± .10	3.92± .98 .54± .07	19.0 ±4.75 2.09± .28
PROPORTIONS OF ULNA					
Proximal width : length	....	9.3–10.3 9.9–11.0	9.94± .11 10.5 ± .04	.31± .08 .21± .03	3.12± .78 2.00± .28
Distal width : length	....	5.2–7.9 7.4–8.6	6.58± .41 7.95± .05	1.16± .29 .28± .04	17.7 ±4.42 3.52± .47

* First row of figures under each category pertains to *californianus*, the second row to *amplus*.

TABLE 5

LENGTH OF THE PHALANGES OF THE WING (mm.)*

	NO. SPEC-IMENS	RANGE	MEAN	STANDARD DEVIATION	COEFFICIENT VARIATION
Digit I	5	38.7–40.5	39.7± .30	.66± .21	1.66± .52
	17	39.1–42.6	41.0± .26	1.06± .18	2.59± .44
Digit II, phalanx 1	6	52.1–54.0	53.4± .23	.56± .16	1.05± .30
	74	51.3–60.5	54.8± .24	2.03± .17	3.70± .30
phalanx 2	4	43.4–44.8	43.9± .31	.62± .22	1.40± .50
	26	47.0–52.9	50.2± .32	1.64± .23	3.27± .45
Digit III	5	34.0–36.2	35.0± .35	.79± .25	2.26± .71
	17	33.3–36.7	34.8± .22	.90± .15	2.59± .44

* First row of figures under each category pertains to *californianus,* the second row to *amplus.*

TABLE 6

MEASUREMENTS (mm.) AND PROPORTIONS OF THE STERNUM*

	NO. SPEC-IMENS	RANGE	MEAN	STANDARD DEVIATION	COEFFICIENT VARIATION
Length	8	148–168	158±2.20	6.26±1.5	3.96± .99
	5	160–176	168±2.10	4.79±1.51	2.85± .90
Keel length	8	126–148	139±2.50	7.20±1.8	5.18±1.30
	9	139–153	147±1.68	5.05±1.19	3.43± .81
Keel height	8	31–36	33.5± .47	1.34± .34	4.00±1.00
	12	32.7–39.8	35.6± .52	1.79± .37	5.03±1.03
Anterior width	7	73–80	75.5±1.08	2.85± .76	3.77±1.01
	6	76–82	79.4± .85	2.07± .60	2.61± .75
PROPORTIONS OF THE STERNUM					
Keel length : length	8	83.1–91.7	87.7±1.10	3.10± .78	3.53± .88
	5	87.1–94.2	89.8±1.19	2.65± .84	2.95± .94
Keel height : keel length	8	22.6–26.2	24.2± .45	1.28± .32	5.29±1.32
	9	23.1–26.9	24.6± .46	1.39± .33	5.65±1.33
Anterior width : length	7	45.9–49.3	47.6± .49	1.30± .35	2.73± .73
	1	45.3	45.3	------------	------------

* First row of figures under each category pertains to *californianus,* the second row to *amplus.*

TABLE 7

MEASUREMENTS OF THE CORACOID (mm.)*

	NO. SPEC-IMENS	RANGE	MEAN	STANDARD DEVIATION	COEFFICIENT VARIATION
Length	22	101–113	109± .63	2.96± .45	2.72± .41
	99	111–128	117± .36	3.58± .25	3.06± .22
Depth shaft	24	9.3–13.9	12.1± .24	1.19± .17	9.83±1.42
	100	10.9–15.8	13.2± .09	.94± .07	7.12± .50
Smallest width shaft	24	13.4–17.4	16.1	------------	------------
	99	14.8–18.9	16.7	------------	------------
Width of head	15	19.9–21.6	20.7	------------	------------
	100	20.0–23.5	21.9	------------	------------

* First row of figures under each category pertains to *californianus,* the second row to *amplus.*

Digit I of the wing is not separable in the two series; the ranges overlap, but the means of total length are statistically different. Length of phalanx 1 of digit II may or may not be a good criterion to separate the species, for tests (Table 15) show that the means and variances could have come from a single stock, although the tests for differences in the means only show them to be significantly different. Phalanx 2 of digit II shows a highly significant difference in mean length between the two series. The length of digit III is in no way significantly different in the series under study (Tables 5 and 15). In all measurements of length of digits the coefficient of variation is greater in *amplus,* but this fact results at least in part from the few specimens of *californianus* that were available. In the latter series the range of the sample is perhaps equivalent to about 70 per cent of the actual range, but in *amplus* the sample is representative of more than 90 per cent of the whole population.

Relatively few specimens of the sternum were available for study (Table 6), but statistically the series of *californianus* may be representative of about 85 per cent of the actual stock. The series for *amplus* exhibits about 85 to 95 per cent of the probable range of variation of the total population. In every measurement of the sternum the ranges overlap. Thus, raw measurements are of no value in distinguishing the two species, although the fossil is larger in each instance. Significance tests (Table 16) on the means of sternal measurements show significant differences. Ratios showing intramembral proportions of the sternum do not vary significantly between the two species (Tables 6 and 16).

TABLE 8

SPREAD OF THE FURCULUM (mm.)

	californianus	*amplus*
Number of specimens	8	10
Range	81–102	92–114
Mean	96.0±2.5	100±2.3
Standard deviation	7.1±1.8	7.3±1.6
Coefficient of variation	7.5±1.9	7.3±1.6

To judge from the extent of the standard deviation, the samples of the coracoids available for the two series are adequate to represent about 95 per cent of the total population. In no raw measurement can individual coracoids of the two forms be distinguished. In the fossil the coracoid is largest in every dimension, but comparable ranges overlap. Results of the significance tests show that the two series differ significantly in their means. The coefficient of variation for coracoidal length is greater in *amplus,* but the V for depth of shaft is larger in *californianus.*

Although the mean spread of the furculum is greatest (Table 7) in *amplus,* the means do not differ significantly (Tables 15 and 16).

The series of scapulae for *californianus* probably are representative of 95 per cent of

TABLE 9

MEASUREMENTS (mm.) AND PROPORTIONS OF THE SCAPULA*

	NO. SPECIMENS	RANGE	MEAN	STANDARD DEVIATION	COEFFICIENT VARIATION
Length	23	105–120	115± .78	3.74± .55	3.25± .48
	11	119–132	124±1.10	3.78± .81	3.05± .65
Width middle of blade	23	9.1–11.9	10.7± .13	.60± .09	5.61± .83
	11	10.7–12.6	11.3± .18	.58± .12	5.13±1.09
PROPORTION					
Width : length	23	7.6–10.3	9.3	....	....
	11	8.2–10.2	9.2	....	....

* First row of figures under each category pertains to *californianus,* the second row to *amplus.*

TABLE 10

MEASUREMENTS OF THE LEG (mm.)*

	NO. SPECIMENS	MEAN	MAX.	MIN.
Femur	19	138	147	132
	100	147	159	136
Tibiotarsus	5	210	213	208
	71	229	244	212
Tarsometatarsus	6	114	117	113
	100	123	134	113
Digit III (total)		100	102	98
		108	120	98
Phalanx 1	3	42.5	43.6	41.9
	72	43.6	48.0	40.8
Phalanx 2	3	30.8	31.3	30.0
	72	34.3	37.8	30.6
Phalanx 3	3	26.4	26.6	26.0
	72	30.2	33.7	26.3
Total length		562	579	551
		607	657	559

* First row of figures under each category pertains to *californianus,* the second row to *amplus.*

the true population. The series for *amplus* includes about 90 per cent of the variants in that species. The means of scapular length and width are greater (Table 9) in the fossil, and tests showed the difference in scapular length to be highly significant (Table 15). There is no significant difference in the ratios of width to length of the scapula. The coefficients of variation for both measurements are greater in *californianus* than in *amplus.*

Leg lengths as shown in Table 10 demonstrate a greater difference between the species than do the wing lengths. Mean leg length in *amplus* is 8 per cent greater than in *californianus;* maximum length is 15 per cent greater in the fossil form, and minimum length is about the same in two species. Ratios of the lengths of the various elements to total leg length show that there is no apparent difference in the proportions of the leg in the two species.

Femora of *californianus* that were measured are characteristic of about 85 to 95 per cent of the total population. The series of femora for *amplus* includes about 95 per cent of the expected range of the actual population (Table 11). Individual femora of either species cannot be identified on the basis of any femoral measurement taken in this study. In each dimension *amplus* is larger, and within the series the differences of the means are highly significant (Table 15). All coefficients of variation (with one exception) are larger in the Recent condor than in the fossil.

The tibiotarsi of the two series are inseparable on the basis of raw measurements (Table 12). Total length and length of fibular crest are greater in *amplus.* It is interesting to note that the distal end of the tibiotarsus is relatively slender in *amplus,* as is the distal end of the ulna. Table 15 shows that the differences in mean length of the tibiotarsi are highly significant. The abnormally low coefficients of variation for

TABLE 11

MEASUREMENTS OF THE FEMUR (mm.)*

	NO. SPECIMENS	RANGE	MEAN	STANDARD DEVIATION	COEFFICIENT VARIATION
Length	19	132–147	138±1.00	4.35± .71	3.15± .51
	100	136–159	147± .40	3.91± .28	2.66± .19
Proximal trans. diameter	19	29.4–34.9	31.1± .33	1.43± .23	4.60± .75
	100	31.9–38.2	34.5± .13	1.30± .09	3.77± .27
Distal trans. diameter	20	33.0–37.2	34.3± .26	1.16± .18	3.38± .53
	99	34.4–40.3	37.0± .12	1.21± .09	3.27± .23
Least diameter shaft	19	14.8–17.4	15.7	----------	----------
	99	14.6–18.4	16.2	----------	----------

* First row of figures under each category pertains to *californianus,* the second row to *amplus.*

TABLE 12

MEASUREMENTS OF THE TIBIOTARSUS (mm.)*

	NO. SPEC-IMENS	RANGE	MEAN	STANDARD DEVIATION	COEFFICIENT VARIATION
Length	5	208–213	210± .90	1.94± .61	.92± .30
	71	212–244	229± .90	7.29± .61	3.18± .27
Proximal width	8	26.2–29.4	27.3	....	....
	----	....	....	....	....
Distal width	6	23.4–25.5	24.3	....	....
	66	22.3–26.2	24.1	....	....
Length fibular crest	6	43.3–47.0	45.1	....	....
	69	42.3–58.8	51.2	....	....

* First row of figures under each category pertains to *californianus*, the second row to *amplus*.

californianus are probably the result of the small sample.

The range of the length of the tarsometatarsus in *californianus* is included in the comparable range in *amplus* (Table 13). However, the sample of the Recent form is small; it is likely that it represents less than 70 per cent of the probable range of the whole population. In no absolute measurement are all individuals of the two series separable. In every dimension the fossil bone averages larger, and these differences are highly significant (Table 15). The coefficient of variation is greater in *amplus* for each of the three measurements, but this probably is a reflection of the small series for the modern condor.

There were so few pedal elements available for *californianus* that statistical analysis was not undertaken. The only statements that can be made regarding the phalanges of the foot are that each phalanx is apparently longer in the fossil and that the coefficients of variation in *amplus* are of a magnitude similar to that found in most zoological series of Recent materials. The greater absolute lengths of the phalanges (as exemplified by those of digit III) in *amplus* were found to be the same relative length as in *californianus* when their means were compared to mean total length of leg.

SUMMARY

In this study it has been found impossible to distinguish the two species, *californianus* and *amplus*, of the cathartid genus *Gymnogyps* on the basis of any qualitative characters in skeletal elements other than those of the skull. Further, it is not possible to segregate all individuals of the two species on the basis of absolute size of skeletal elements. In no measurement made in this

TABLE 13

MEASUREMENTS OF THE TARSOMETATARSUS (mm.)*

	NO. SPEC-IMENS	RANGE	MEAN	STANDARD DEVIATION	COEFFICIENT VARIATION
Length	6	113–117	114± .71	1.75± .51	1.54± .44
	100	113–134	123± .40	3.96± .28	3.22± .23
Diameter through cotyla	6	25.5–28.0	26.6± .38	.94± .27	3.53±1.02
	86	26.5–31.7	28.5± .13	1.16± .09	4.07± .31
Diameter through trochlea	6	28.3–30.2	29.4± .31	.75± .22	2.55± .74
	97	29.5–34.5	32.2± .17	1.64± .12	5.09± .37

* First row of figures under each category pertains to *californianus*, the second row to *amplus*.

TABLE 14

LENGTH OF PHALANGES OF FOOT (mm.)*

	NO. SPEC-IMENS	RANGE	MEAN	STANDARD DEVIATION	COEFFICIENT VARIATION
Digit I, phalanx 1	3	22.9–24.5	23.6	-------	-------
	24	22.2–27.9	25.1± .28	1.35± .19	5.38± .78
Digit II, phalanx 1	3	30.2–31.0	30.6	-------	-------
	72	29.7–35.1	33.0± .16	1.40± .12	4.24± .35
phalanx 2	3	24.6–25.2	24.8	-------	-------
	49	24.8–29.9	27.3± .19	1.35± .14	4.95± .50
Digit III, phalanx 1	3	41.9–43.6	42.5	-------	-------
	72	40.8–48.0	43.6± .35	2.95± .25	6.77± .56
phalanx 2	3	30.0–31.3	30.8	-------	-------
	72	30.6–37.8	34.3± .17	1.41± .12	4.11± .34
phalanx 3	3	26.0–26.6	26.4	-------	-------
	72	26.3–33.7	30.2± .19	1.61± .13	5.33± .44
Digit IV, phalanx 1	3	23.0–24.0	23.4	-------	-------
	60	22.6–26.9	24.4± .13	1.00± .09	4.10± .37
phalanx 2	1	15.9	15.9	-------	-------
	10	16.5–18.7	17.7± .21	.66± .15	3.73± .83
phalanx 3	1	12.9	12.9	-------	-------
	6	13.0–14.5	13.8± .21	.51± .15	3.69±1.07
phalanx 4	2	16.3–16.4	16.4	-------	-------
	3	18.2–18.9	18.6	-------	-------

* First row of figures under each category pertains to *californianus,* the second row to *amplus.*

TABLE 15

RESULTS OF SIGNIFICANCE TESTS*

	DIFF. IN MEANS AND VARI-ANCES	P	DIFF. IN MEANS ONLY	P
Humeral length	3.95	0.0001	5.88	0.0001
Proximal width humerus	6.27	.0001	6.96	.0001
Length deltoid crest	9.88	.0001	7.66	.0001
Proximal width humerus : humeral length	10.17	.0001	6.75	.0001
Length deltoid crest : humeral length	9.87	.0001	7.67	.0001
Ulnar length	2.04	.05	3.20	.001
Proximal width ulna	5.72	.0001	5.94	.0001
Distal width ulna	6.79	.0001	3.73	.001
Proximal width ulna : ulnar length	5.95	.0001	4.79	.0001
Distal width ulna : ulnar length	5.75	.0001	3.32	.001
Metacarpal length	3.01	.001	9.81	.0001
Digit I of wing	2.57	.01	3.28	.001
Digit II, phalanx 1, wing	1.66	.09	4.21	.0001
Digit II, phalanx 2, wing	7.64	.0001	14.14	.0001
Digit III of wing	0.45	.66	0.48	.63
Coracoidal length	9.76	.0001	11.03	.0001
Coracoid, depth of shaft	5.04	.0001	4.29	.0001
Furcular spread	1.12	.24	1.13	.23
Scapular length	6.62	.0001	6.67	.0001
Femoral length	8.86	.0001	8.36	.0001
Proximal width of femur	9.99	.0001	9.59	.0001
Distal width of femur	9.27	.0001	9.43	.0001
Tibiotarsal length	5.59	.0001	14.94	.0001
Tarsometatarsal length	5.48	.0001	11.04	.0001
Diameter through cotyla of tarsometatarsus	3.78	.0001	4.73	.0001
Diameter through trochlea of tarsometatarsus	4.07	0.0001	7.92	0.0001

* Formula 1 (p. 228) was used for the test of difference in both means and variances, and Formula 2 (p. 228) was used to test for significant differences in the means. Specific values are given only for those probabilities of a magnitude greater than 1 in 10,000. All others are simply listed as less than 1 in 10,000.

study is there a gap between ranges of comparable measurements that would make this segregation feasible. In all elements where there is a difference in average size, *amplus* is the larger, except for the distal widths of the ulna and tibiotarsus. Extremely large or small specimens can be allocated in most instances to *amplus* and *californianus*, respectively.

Ratios designed to show the proportions of the bones cannot be used as a means of differentiation for individual bones. In general, the bones are sturdier in the fossil form, but the ranges of comparable ratios in the two series consistently overlap.

Despite this inability to separate the two series, the significance tests made on the means of 34 different measurements and ratios demonstrate conclusively that we are dealing with two distinct forms which, in most measurements, have significantly different means. Only 5 of the 34 tests failed to indicate significant differences between the means and the two populations represented by them. These 5 tests were on length of digit III of the wing, furcular spread, and two ratios on sternal proportions. However, the significance test on both the means and variances shows also that length of ulna, length of digit I of wing, and length of phalanx 1 of digit II are not significantly different.

TABLE 16

RESULTS OF SIGNIFICANCE (t) TESTS ON MEANS

	t	P
Sternal length	2.84	$<.02$
Keel length	2.54	$>.02$
Keel height	2.68	$<.02$
Keel, anterior width	2.55	$>.02$
Keel length : total length	1.21	$>.10$
Keel height : keel length	0.58	$>.10$
Width scapular blade	2.58	$>.02$
Spread of furculum	1.10	$>.10$

Gymnogyps amplus was found to be no more variable than *G. californianus*. The coefficient of variation was calculated for 33 identical measurements and ratios in each species. In 18 ratios and measurements the V was greater in *californianus* than in *amplus*; in 15 instances the reverse was true. The mean V for *amplus* was 3.56 and that for *californianus* was 4.30. The relatively small samples of several elements for *californianus* in all probability reduced the coefficient of variation disproportionately in this species, although the V for two elements was abnormally high. In one series (phalanges of the foot) where it seemed impractical to calculate the coefficient of variation for *californianus*, all the coefficients in the large series for *amplus* were similar to those usually found in zoological series. Because coefficients of variation of linear measurements and of ratios are not comparable, the Vs were separated. In the Recent species the average V for linear measurements was 4.00, compared to 3.69 for the fossil. The Vs for the ratios were 5.45 for *californianus* and 2.98 for *amplus*. To make the comparison even more reliable, only those pairs of Vs based on samples of 10 or more linear measurements were included in the last examination of these coefficients; the average V was 4.32 in *californianus* and 3.78 in *amplus*. Further, in only three of the pairs in this analysis was the V higher in the Pleistocene species. Therefore, for *Gymnogyps* at least, Pleistocene and Recent species show no major differences in total variability.

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